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Herbivory on freshwater and marine macrophytes: a review and perspective

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Abstract

Until the 1990s, herbivory on aquatic vascular plants was considered to be of minor importance, and the predominant view was that freshwater and marine macrophytes did not take part in the food web: their primary fate was the detritivorous pathway. In the last 25 years, a substantial body of evidence has developed that shows that herbivory is an important factor in the ecology of vascular macrophytes across freshwater and marine habitats. Herbivores remove on average 40-48% of plant biomass in freshwater and marine ecosystems, which is typically 5-10 times greater than reported for terrestrial ecosystems. This may be explained by the lower C:N stoichiometry found in submerged plants. Herbivores affect plant abundance and species composition by grazing and bioturbation and therewith alter the functioning of aquatic ecosystems, including biogeochemical cycling, carbon stocks and primary production, transport of nutrients and propagules across ecosystem boundaries, habitat for other organisms and the level of shoreline protection by macrophyte beds.

With ongoing global environmental change, herbivore impacts are predicted to increase. There are pressing needs to improve our management of undesirable herbivore impacts on macrophytes (e.g. leading to an ecosystem collapse), and the conflicts between people associated with the impacts of charismatic mega-herbivores. While simultaneously, the long-term future of maintaining both viable herbivore populations and plant beds should be addressed, as both belong in complete ecosystems and have co-evolved in these long before the increasing influence of man. Better integration of the freshwater, marine, and terrestrial herbivory literatures would greatly benefit future research efforts.

Keywords: climate change, conservation, ecosystem functions, grazing, seagrass, stoichiometry

1. Introduction: 25 years of research on herbivory on macrophytes

1.1 *Setting the scene*

In the 1990s two seminal papers appeared in Aquatic Botany that urged for a complete change in the paradigm that had been dominating macrophyte ecology. Despite some early work on the impact of waterbirds on freshwater and marine angiosperms (Jupp and Spence, 1977; Jacobs et al., 1981), until then, herbivory on aquatic vascular plants was considered to be of minor importance, and the predominant view was that freshwater and marine macrophytes did not take part in the food web (e.g. Shelford (1918) and their primary fate was the detritivorous pathway (Polunin, 1984; Duarte and Cebrian, 1996). But in 1991, Lodge argued that, contrary to conventional wisdom, live freshwater macrophytes are engaged in aquatic food webs. In 1998, Cebrian and Duarte highlighted that, while seagrasses suffered modest herbivory rates on average, such rates were highly variable, and the importance of seagrass-herbivore interactions should not be discounted. Following on from these two papers, Lodge (1998) provided further evidence for the important role of herbivores in freshwater habitats, as compared to other biomes; and Valentine and Heck (1999) demonstrated that grazing on seagrasses is widespread in the world's oceans.

Together, these landmark papers put macrophyte herbivory on the map. Since then, there has been a strong increase in the amount of studies that investigated herbivory on freshwater macrophytes and seagrasses. In this study, we review what we have learned in the 25 years that followed the appearance of Lodge (1991). Furthermore, we identify new topics that have emerged over this time. These new topics include the fast changes that may occur in macrophyte-herbivore relationships with the ongoing global environmental change, as well as the potential conflicts between herbivore conservation and herbivore impacts on aquatic ecosystems. Finally, we discuss how we can improve our understanding of herbivore impacts and what tools may help us in

achieving this. Following the approach of the seminal papers listed above, we focus primarily on aquatic angiosperms (submerged, floating and emergent) and address both freshwater and marine ecosystems.

1.2 *Why thinking about herbivory on macrophytes has changed over the last 25 years*

The paradigm shift in our perception of macrophyte herbivory, from being considered negligible to being acknowledged as a key factor shaping benthic ecosystems, is not only caused by an increase in scientific interest fostered by these landmark papers: the effect of herbivory became also more conspicuous over the last 25 years. The reasons for this are methodological, anthropogenic and ecological.

Methodological improvements for estimating herbivory included observation methods, such as bite mark counts (Cebrian and Duarte, 1998), experimental approaches, such as herbivore exclusions (see Poore et al. (2012) and Wood et al. (2016) for syntheses of marine and freshwater habitats, including macro-algae) and direct methods, including video bite counts or isotopic signatures (see Table 4 for details).

Anthropogenic effects included increases in the densities of aquatic and marine herbivores as a result of increased protection, predator removal, food subsidies from agriculture, and the introduction of exotic herbivores (Estes et al., 2011). For example, steep increases in herbivory rates have been reported for sea turtles in the Arabian Sea and Indonesia (Kelkar et al., 2013b, a), (Christianen et al., 2014), for herbivorous fish in the Mediterranean (Pages et al., 2012) and for geese in Northwestern Europe and North America (Jefferies et al., 2003; Van Eerden et al., 2005). However, it should be noted that despite recent local increases in herbivory, which have attracted attention to the role of herbivores in benthic ecosystems, over longer time frames in particularly species of large herbivores have experienced strong global declines (Jackson, 1997; McCauley et al., 2015; Bakker et al. 2016b).

116 Furthermore, the recent spread of exotic herbivores had major consequences for
117 macrophyte establishment and survival in many areas worldwide. For example, tropical lessepsian
118 rabbitfishes (*Siganus spp.*) cause overgrazing of macroalgae and seagrasses at the Eastern
119 Mediterranean (Verges et al., 2014b), chubs and rabbit fishes (*Kyphosus* spp. and *Siganus* spp.,
120 Siganidae) overgraze Australian and Japanese kelp forests (Verges et al., 2014a), North-American red-
121 swamp crayfish (*Procambarus clarkii*) have depleted submerged plant meadows in shallow lakes
122 across Europe (Rodriguez et al., 2003; Gherardi and Acquistapace, 2007; van der Wal et al., 2013),
123 and intentional introductions of grass carp (*Ctenopharyngodon idella*) have been considered a threat
124 to native macrophytes (Wittmann et al., 2014).
125 Ecological effects are related to the oligotrophication of many European freshwater systems,
126 which resulted in their re-colonization with submerged macrophytes (Jeppesen et al., 2005). In many
127 systems, however, the impact of aquatic herbivores sufficed to halt or reverse such recolonization
128 (Körner and Dugdale, 2003; Hilt, 2006; Bakker et al., 2013; Hilt et al., 2013; Eigemann et al., 2016).
129
130
131 **2. Quantitative impacts of herbivores in aquatic systems**

132 *2.1. Quantitative impact of herbivores on plant biomass across ecosystems*

133 A growing body of primary research has demonstrated herbivore-induced changes in one or
134 more measures of macrophyte abundance, including biomass, two-dimensional cover, volume, and
135 individual density (Kirsch et al., 2002; Marklund et al., 2002; Tomas et al., 2005; Prado et al., 2007;
136 Christianen et al., 2012; Pages et al., 2012; Wood et al., 2012a; Kelkar et al., 2013b, a; Christianen et
137 al., 2014; Bakker et al., 2016b). These studies, synthesized in several reviews (Cyr and Pace, 1993;
138 Valentine and Duffy, 2006; Gruner et al., 2008; Poore et al., 2012), confirmed herbivores as key
139 drivers of benthic ecosystems around the world. The overwhelming majority of studies reported a
140 reduction in macrophyte abundance as a result of herbivory. Indeed, a recent meta-analysis of 326

141 experiments in which freshwater herbivores were excluded found that herbivory reduced
142 macrophyte biomass by 47.2 ± 3.4 % (average ± CI) (Wood et al., 2016). Of these, 300 experiments
143 reported a reduction in macrophyte biomass, while 26 experiments reported positive effects or no
144 changes. Similarly, a meta-analysis on grazing impacts on marine macrophytes found that herbivores
145 reduce macrophyte abundance (both submerged angiosperms and macro-algae) by 68% on average
146 (Poore et al., 2012).

147 Despite their historical disregard, the removal of vascular plant biomass by herbivores is, on average,
148 much larger in aquatic than in terrestrial ecosystems. The most recent meta-analyses available for
149 terrestrial, freshwater and marine habitats (Turcotte et al., 2014; Wood et al., 2016) show that
150 median biomass removal by herbivores is 4-8 % in terrestrial ecosystems, while it is 44-48% in
151 freshwater and 40-44% in marine ecosystems (Fig 1a-c). Thus, herbivores remove on average 5-10
152 times more vascular plant biomass in aquatic ecosystems than in terrestrial ones.

153 Yet, the impact of herbivores on vascular plant biomass removal is much more variable in aquatic
154 than in terrestrial ecosystems, and it ranges as broadly as between 0 and 100% of biomass removal
155 (Fig 1a-c). Underlying explanations for the large range of herbivore effects in aquatic ecosystems are
156 still unknown. Potential mechanisms involve bottom-up effects, such as variation in plant
157 productivity, nutritional quality, stoichiometry, resistance and tolerance to grazing (Cebrian et al.,
158 2009); and top-down effects, such as variation in herbivore abundance, feeding efficiency, size,
159 taxonomy, mobility, metabolism and predator effects (Borer et al., 2005).

160

161 ### *2.2. Bottom-up effects: the plant's perspective*

162 #### *2.2.1. Primary productivity and herbivory rates*

163 Studies in aquatic systems traditionally focussed on primary production of phytoplankton in pelagic
164 habitats, and only recently littoral areas received more attention (Vadeboncoeur et al., 2002;

165 Brothers et al., 2013). Theoretical predictions based on Lotka-Volterra models suggest that grazing
166 should increase with primary productivity (Gruner et al., 2008), because as plants produce more
167 tissues or do so at faster rates, herbivores can increase their rates of consumption. This prediction
168 relies in the assumption that herbivory rates are bottom-up regulated by the availability of plant
169 tissues. Empirical evidence is however conflicting. A meta-analysis by Cyr and Pace (1993) concluded
170 that herbivory increases with primary production in both terrestrial and aquatic systems. However, a
171 more recent meta-analysis found no significant effect of productivity on herbivory (or interaction
172 strength) in aquatic systems (e.g. (Borer et al., 2005)). In fact, it is widely recognized that food quality
173 and defences also have major effects on herbivore performance that might mask any herbivory-
174 productivity relationship. Using a plant growth model, Hidding et al. (2016) suggested that herbivore
175 grazing effects on macrophytes become important above certain thresholds in periphyton shading
176 and thus reduced production of plants.

177

178 *2.2.2. Plant stoichiometry*

179 Differences in herbivory rates across plant taxa have also been attributed to differences in
180 plant quality, as perceived by herbivores (Lodge, 1991; Cronin et al., 2002). Generally, there is a
181 positive relationship between the nitrogen content in the plant's tissue and its consumption by
182 herbivores (Cebrian and Lartigue, 2004). This pattern holds both within and across ecosystems (Elser
183 et al., 2000; Cebrian and Lartigue, 2004; Cebrian et al., 2009). Hence, it has been suggested that
184 higher herbivore consumption rates in aquatic plants might be explained by their higher quality as
185 food – arising from the lack of carbon-rich structural compounds that strengthen cell walls, increase
186 resistance to herbivores, and reduce digestibility in terrestrial plants (Gruner et al., 2008).
187 Unfortunately, most comparisons between aquatic and terrestrial systems undertaken to date
188 restricted their estimates of aquatic herbivory to phytoplankton consumption, thus giving limited or
189 no information on the consumption of aquatic macrophytes (Elser et al., 2000). Comparing herbivory

190 rates on, and food quality (e.g., nitrogen content) of, aquatic and terrestrial vascular plants would be
191 more informative, because they have a close phylogenetic affinity and most differences could be
192 attributed to the ecosystems they inhabit (Hay, 1991; Gross and Bakker, 2012; Burkepile, 2013).

193 A compilation of data on C:N ratios of vascular plants in terrestrial, freshwater and marine
194 ecosystems reveals that they differ strongly between these systems (Fig 1d-f). Median C:N ratio
195 decreased strongly from terrestrial vascular plants (25-30) and marine macrophytes (24-28) to
196 freshwater macrophytes (12-16) (Fig 1d-f). The high N content (thus low C:N ratio) of freshwater
197 macrophytes may indicate a higher quality to herbivores, potentially explaining the high herbivory
198 rates found in freshwater systems. Taking into account the variation in growth forms that occurs in
199 aquatic ecosystems makes this pattern stronger (Fig 2a-d). Herbivory rates are lower on emergent
200 macrophytes (median freshwater = 36-48%; median marine = 24-36%) than on submerged
201 macrophytes (median freshwater and marine = 48-60%) in both freshwater and marine ecosystems
202 (Fig 2a,b). These differences fit closely the C:N ratio of the different plant growth forms, as emergent
203 macrophytes have higher C:N ratios (median freshwater = 28-32; median marine = 24-28) than
204 submerged macrophytes (median freshwater = 8-12; median marine = 20-24), particularly in
205 freshwater ecosystems (Fig 2c,d).

206 Our data compilation indicates that differences in plant quality between terrestrial plants
207 and macrophytes show close links to variation in herbivory rates. Submerged plants need less
208 structural components, resulting in higher N content and higher rates of herbivory. In contrast,
209 herbivory rates and N content of emergent macrophytes are similar to those found in terrestrial
210 plants (Fig 1a, 1d, 2a-d). Although N content is acknowledged as an important determinant of plant
211 quality to herbivores, other nutrients and secondary compounds may also influence it. For example,
212 freshwater macrophytes and seagrassess have anti-herbivore defenses (Verges et al., 2008; Gross
213 and Bakker, 2012), which may cause low palatability - even in highly nutritious species. Phenolics,
214 terpenoids and nitrogenated compounds can be efficient deterrents of aquatic herbivores, although

deterrence of generalist herbivores often comes at the cost of higher preference by specialised consumers (Verges et al., 2007). Interestingly, in freshwater systems, the concentrations of phenolic compounds decrease from emergent to floating to submerged plants (Smolders et al., 2000), suggesting not only higher nutritional quality, but also less defended tissues, resulting in generally higher palatability of submerged plants. However, this issue still deserves more research, since most work has focused on macro-algae (e.g. (Hay, 1996)). Besides the differences between ecosystems discussed above, spatial and temporal variation in herbivory at population and individual-plant level has also been linked to plant quality (C:N, % N) and to the presence of anti-herbivore defences (Hacker and Bertness, 1995; Preen, 1995; Verges et al., 2007; Prado et al., 2010).

2.3. Top-down effects: the herbivore's perspective

2.3.1. Herbivore density

Within individual herbivore species, herbivore impact on aquatic plant abundance is positively related to herbivore density (Stott and Robson, 1970; Valentine and Heck, 1991; Wood et al., 2012a; Kelkar et al., 2013b). However, analyses of herbivore impacts across multiple herbivore species have found no relationship between herbivore density and macrophyte abundance, probably due to the confounding effects of interspecific differences in herbivore ecology (Marklund et al., 2002; Wood et al., 2012a). For example, among plant-eating waterfowl, substantial differences exist in mean adult body mass (from the 24 g of ocellated crake, *Micropygia schomburgkii*, to the 12,000 g of trumpeter swan, *Cygnus buccinator*), which is known to influence the species' diet and the absolute quantity of vegetation consumed (Wood et al., 2012a). Consequently, when herbivore densities were estimated as biomass densities (thus accounting for interspecific differences in individual body mass), a significant negative relationship between herbivore biomass density and macrophyte abundance was detected (Wood et al., 2012a; Wood et al., 2016). Only at relatively low herbivore densities were

positive changes in plant abundance reported, suggesting that in aquatic systems greater herbivore densities overwhelm plant compensatory growth responses (Wood et al., 2016).

2.3.2. Size, mobility and taxonomy of herbivores

By virtue of their size, large terrestrial herbivores are critical agents of change and maintenance of the ecosystems they inhabit (Owen-Smith, 1988; Bakker et al., 2016a). In aquatic environments, large herbivores have also been identified as key species (McCauley et al., 2015), often considered ecosystem engineers (e.g. (Bakker et al., 2016b)). It is not surprising, thus, that a recent meta-analysis found significantly stronger impacts of macrograzers (fishes, urchins and large molluscs) than mesograzers (amphipods, isopods and small molluscs) on marine macrophytes (algae, seagrasses and salt marshes) (Poore et al., 2012).

Another recent meta-analysis by Wood et al (2016) found substantial between-taxa differences in effects of herbivores on the abundance of freshwater and marine macrophytes. Echinoderms, molluscs, and fish had relatively large impacts on plants, while insects and birds had relatively low impacts. The reason for these differences may be the mobility and habitat preferences of each of these groups. Fully aquatic species that live underwater permanently, have been shown to produce the greatest impacts on aquatic plants (Bakker et al., 2016b), while facultative aquatic grazers, such as insects and birds, spread their activity more between different ecosystems (thanks to their high mobility), thus spreading also their impact between such ecosystems. Wood et al. (2016) also pointed out the fact that some herbivores (such as echinoderms, crayfish and molluscs) have restricted mobility and produce intense impacts due to their bulk grazing strategies, since they consume multiple tissues types and species, thus affecting a greater proportion of a plant community (Lodge et al., 1998).

2.3.3. *Herbivory and omnivory*

Most animals that consume aquatic plants are omnivores, very few are strict herbivores. There is a positive relationship between body size and degree of herbivory in aquatic omnivores: the larger the consumer, the more important plant consumption (granivory and folivory, particularly the latter) is in their diet (Clements et al., 2009; Wood et al., 2012a). Hence, per capita, large herbivores have the largest impact on plant abundance through grazing. The high level of generalistic feeding and omnivory of aquatic plant consumers may be related to the higher impact of herbivory on aquatic plants, because it may relax the effect of direct density dependence on consumers: whenever consumers overgraze plants, they can switch to alternative food sources (algae, detritus or animal prey) within or nearby the water body (Grey and Jackson, 2012). Furthermore, in aquatic systems, large herbivores and omnivores often feed on both aboveground and belowground plant material, which may multiply their impact on plants, due to the depletion of underground plant resources for regrowth.

Herbivore impact may also be enhanced by non-consumptive effects, which are documented to be severe in freshwater and marine macrophytes, e.g. bioturbation (Lodge, 1991). By initiating bare patches, herbivores can create focal points for further erosion of macrophyte meadows by waves in shallow areas (Christianen et al., 2013). Trampling, fecal deposition and increasing nutrient concentrations may also play a role. Whilst previous authors have cautioned against the assumption that herbivore effects on plants represent exclusively grazing losses due to consumption (Mitchell and Wass, 1996b), many studies continue to ignore the roles of non-consumptive effects.

2.4. *Latitude*

Potential variance in herbivore impacts on plant abundance across different latitudes has been a topic of growing interest among ecologists. However, the evidence for a role of latitudinal effects is

limited. For example, in macrophyte feeding assays carried out by Morrison and Hay (2012), only one out of three crayfish species showed a preference associated with latitude (a preference for higher latitude plants). Schemske et al. (2009) argued that, across all ecosystems, herbivore impacts are greater at lower latitudes. In contrast, a meta-analysis by Gruner et al. (2008) reported an increase in herbivore effects at higher latitudes in freshwater ecosystems, but not in marine ecosystems. Three more recent meta-analyses with larger sample sizes found no evidence of latitudinal gradients in herbivore impacts on aquatic macrophyte abundances, some including both vascular plants and macro-algae (Moles et al., 2011; Poore et al., 2012; Wood et al., 2016).

3. Ecosystem consequences of herbivory

With the establishment of herbivory as a an important factor regulating plant abundance, Lodge (1991) ended his review with the conclusion that "the functional importance of grazing remains largely untested". Indeed, this has been an emerging field of research over the last 25 years, with particular progress over the last 5 years. By their presence, herbivores may induce direct changes in plant dynamics and indirect effects on ecosystem functioning (Fig. 3). The effects of marine herbivores may include stimulated production of seagrass (Valentine et al., 1997; Moran and Bjorndal, 2005; Vonk et al., 2008b; Christianen et al., 2012), changes in seagrass meadow structure (Lal et al., 2010), and the reduction of the flux of organic matter and nutrients to sediments and plants (by short circuiting the detrital cycle; (Thayer et al., 1982; Vonk et al., 2008a) or their export to nearby habitats (Christianen et al., 2012). In salt marshes and aquatic ecosystems, an additional effect of herbivores is the return of nutrients through faeces and urine (Bazely and Jefferies, 1985; Hik et al., 1991; Frank et al., 2000), though in seagrass grazed by turtles this effect is reduced by nutrient transport to turtle resting areas (Christianen et al., 2012).

3.1 *Plant abundance and species composition and diversity*

While the largely negative impacts of herbivores on macrophyte abundance have been well documented through short-term exclosure studies, the persistence of such effects it is often less clear. In particular, highly-mobile herbivores such as waterfowl can cause large reductions in plant abundance before switching to ungrazed sites (Wood et al., 2012b). Ecosystem responses to fluctuating grazing pressure have received little attention to date. However, there is some evidence that repeated episodes of grazing over time, such as by breeding colonies of snow geese (*Chen caerulescens*) in wetlands, can cause sustained long-term shifts in species composition and declines in plant abundance (Kerbes et al., 1990). Where non-selective, generalist herbivores feed on mixed assemblages of macrophyte, herbivores can increase species evenness by reducing the abundance of dominant competitors relative to sub-dominant macrophyte species (Hidding et al., 2010b; Wood et al., 2012b). However, when they favor certain subordinate plant species over the dominant, they can reduce eveness (Hidding et al. 2010a).

Herbivory in tropical seagrasses (e.g. by sea urchins and green turtles) can influence species composition (Vonk et al., 2008b; Kelkar et al., 2013b; Hernandez and van Tussenbroek, 2014), but often in contrasting ways. In tropical multispecies meadows, slow growing climax seagrass species (*Thalassia hemprichii*) were promoted by small herbivores (urchins), while in more intensively grazed meadows species difference in herbivore's grazing preferences resulted in the dominance of fast growing pioneer species (Kelkar et al., 2013b). Larger grazers that consume belowground plant parts and create bare sediment patches, such as green turtles and dugongs, also introduce species heterogeneity by setting back species succession in grazed plots (Aragones et al., 2006; Christianen et al., 2013).

3.2 *Ecosystem functions and services of aquatic herbivores*

335 *3.2.1. Seed and propagule dispersal*

336 Besides their direct effects on their food plants, aquatic herbivores provide a key service for aquatic
337 ecosystems: the passive dispersal of a broad variety of aquatic organisms, including the
338 aforementioned food plants, as well as many other taxa attached or associated to them (Figuerola
339 and Green, 2002a; Brochet et al., 2010a; van Leeuwen et al., 2012). Dispersal by most inland-water
340 herbivores contributes to the redistribution of individuals within single wetlands and among nearby
341 ones; while waterbirds (most notably, migratory species) are the main vector of long-distance
342 dispersal among wetlands situated at separated watersheds, from regional to continental scales
343 (Viana et al., 2013b; Viana et al., in press). Among waterbirds, the frequency and scale of long-
344 distance dispersal events is known to vary with the vector's morphology, to depend on the migratory
345 strategy and to scale negative with body mass (Green and Figuerola, 2005; Viana et al., 2013b; Viana
346 et al., 2013a). In the marine environment, biotic dispersal by herbivores (sea turtles, ducks and fish)
347 has been reported for seagrasses (Sumoski and Orth, 2012) and passive transport of other organisms
348 is also known to occur (e.g. sessile invertebrates transported by sea turtles and crabs (Winston,
349 2012). The opposite process may also take place – e.g. anecdotal evidence suggests that green turtle
350 hatchlings use kelp rafts for passive dispersal (Carr and Meylan, 1980).

351 In terrestrial systems, animal-mediated dispersal is often facilitated by rewards encasing the
352 propagules or attached to the seeds (such as fruits, elaiosomes and some pods). In contrast, aquatic
353 plant seeds typically lack rewards; hence, their dispersal is mediated by the ingestion of plant
354 vegetative parts by herbivores (´foliage in the fruit´, sensu Janzen (1984)), the occasional survival of
355 seeds ingested by granivores (e.g. teals (Brochet et al., 2010b)) or the accidental ingestion of seeds
356 by carnivores/omnivores (notably filter-feeders, such as flamingoes and shovelers (Verhoeven, 1980;
357 Figuerola et al., 2003). This difference results in major differences in selection pressures, which can
358 be traced to differences in predominant seed traits (Table 1). Aquatic plant seeds are typically small,
359 which facilitates their ingestion mixed with the foliage, their survival to gut passage, and a prolonged

360 gut-passage times resulting in longer dispersal distances (Mueller and van der Valk, 2002;
361 Charalambidou and Santamaria, 2005; Soons et al., 2008; Figuerola et al., 2010). Larger seeds often
362 have thick and impermeable coats, necessary to withstand their severe scarification in waterbird guts
363 (which tend to retain selectively such larger seeds(Kleyheeg, 2015) and the severe physico-chemical
364 treatment exerted by their guts (Figuerola et al., 2002; Santamaria et al., 2002). Such coat types
365 often result in strong physical dormancies, which may postpone seed germination until ingestion by a
366 potential dispersal vector has taken place (e.g. in seeds collected from the sediment bank by
367 granivores and filter feeders (Figuerola et al., 2003). Invertebrate propagules dispersed by waterfowl
368 typically show similar traits: small size, one to several protective coats, and delayed or stochastic
369 hatching (Charalambidou and Santamaria, 2002). In some cases, the encasement of resting eggs in
370 the mother's body may provide both protection against their digestion and a reward to potential
371 dispersers – having thus a function analogous to that of plant fruits, whose functional and adaptive
372 value of such a trait remains to be studied.

373 External dispersal may take place attached to the animal's fur or plumage, or adhered to mud-
374 stained surfaces in the body or feet (Figuerola and Green, 2002b; Frisch et al., 2007). Available
375 evidence suggests, however, that it is less frequent than internal dispersal (Brochet et al., 2010b).
376 Once again, small propagules are much more likely to become attached or adhered, and remain in
377 such situation long enough for long-distance dispersal to occur. Other traits that have been generally
378 assumed to facilitate external dispersal, such as flat shapes and suitable surface structures (hooks,
379 thorns, hairs), are known to occur in plant and invertebrate propagules (e.g. Vivian-Smith and Stiles
380 (1994)). As above, their functional and adaptive value remains to be studied.

381 Propagule dispersal, particularly over long distances, influences the population, genetic and
382 community structure of aquatic organisms (Viana et al., 2014). Hence, it is broadly regarded as a key
383 ecosystem service provided by aquatic herbivores. Its effect is, however, more evident when such
384 immigrants encounter empty niches (e.g. colonization of disturbed, new or restored wetlands) than

385 when they face resident genotypes or species, established before their arrival (Louette and De
386 Meester, 2005). In such cases, the immigrant's establishment may be precluded by biotic resistance
387 arising from intra- and inter-specific competition, mortality caused by natural enemies and
388 environmental filtering (e.g. habitat changes caused by other species). Even then, the process of
389 propagule dispersal represents a key element of ecosystem resilience – particularly in inland waters,
390 which are fragmented and isolated by nature. Such resilience may prove vital, in the near future, for
391 ecosystem adaptation to global change – by facilitating rapid range shifts and the readjustment of
392 genetic structure (e.g. locally-adapted genotypes) caused by the accelerating changes in
393 environmental conditions associated to global warming, land use changes and the perturbation of
394 global nutrient cycles (Amezaga et al., 2002; Röckstrom et al., 2009; Robledo-Arnuncio et al., 2014).

395 Propagule dispersal by aquatic herbivores may also entail negative effects for native species and
396 ecosystems when it mediates the arrival and spread of alien species (Reynolds et al., 2015). Examples
397 include both plant and invertebrate species (Charalambidou et al., 2003; Brochet et al., 2009; Munoz
398 et al., 2013), although the effect of dispersal on human-mediated dispersal is often predominant or
399 difficult to disentangle (Weisz and Yan, 2010; Van Leeuwen et al., 2013). It is also worth noting that,
400 despite their potential role as seed dispersers, aquatic herbivores may also reduce the frequency of
401 propagule dispersal by reducing propagule production – due to the consumption of plant vegetative
402 parts (e.g. (Wood et al., 2012a; Darnell and Dunton, 2015)) and the invertebrates attached or
403 associated to them.

404

405 *3.2.2 Biogeochemical cycling*

406 Grazing and bioturbation by aquatic herbivores can have direct and indirect effects on
407 biogeochemical cycling. In oligotrophic systems, grazing by smaller herbivores can have positive
408 effects by conserving nutrients within the meadow and closing the cycling of nutrients from leaf
409 material. Leaf material can be shredded (sea urchins, (Vonk et al., 2008b)), burrowed (Alpheid

410 shrimp, (Vonk et al., 2008a)) or excreted after grazing (fish, (Kirsch et al., 2002)), thus stimulating
411 nutrient retention. Larger herbivores such as green turtles and dugongs may travel between different
412 habitats and stimulate export of nutrients between foraging (seagrass) and resting (coral reefs) areas
413 (Christianen et al., 2012).

414 By foraging and resting in terrestrial and aquatic environments, herbivores provide aquatic-terrestrial
415 linkages, transporting carbon, nutrients and contaminants from land to water (for instance
416 hippopotamus *Hippopotamus amphibius* (Subalusky et al., 2015), waterbirds (Hahn et al., 2008;
417 Chaichana et al., 2010) or large savanna herbivores(Moss, 2015) or *vice versa* (for instance by moose
418 *Alces sp.* (Bump et al., 2009)). It has recently been suggested that the decline in large herbivore
419 densities and the extinction of Late Pleistocene megafauna caused a strong reduction in the capacity
420 of transport of phosphorus from nutrient hotspots, such as streams or floodplains, towards less
421 fertile inland areas (Doughty et al., 2016). Long distance travel of migratory herbivores also
422 contributes to transport of nutrients across sites of varying fertility (Bauer and Hoye, 2014).

423 In seagrass meadows, grazing by mesoherbivores can increase productivity and possibly carbon
424 sequestration. However below-ground grazing (e.g. by dense populations of green turtles) or other
425 factors of disturbance in the seagrass root mat can cause release of ancient carbon, which may
426 contribute to increased global warming (Macreadie et al., 2015). Similarly, early season below-
427 ground foraging by pink-footed geese (*Anser brachyrhynchus*) is sufficient to strongly reduce C sink
428 strength and soil C stocks of arctic tundra (van der Wal et al., 2007). Recent studies are therefore
429 stressing that it is critical to maintain intact predator populations that control large herbivore
430 densities to prevent grazer aggregation, protect carbon stocks and avoid seagrass meadow collapse
431 (Atwood et al., 2015). In a subtropical seagrass ecosystem, large predators (e.g. tiger sharks) induce
432 plant species shifts by changing the foraging tactics of large grazers, such as turtle and dugongs
433 (Heithaus et al., 2007). Under low predation risk, dugongs and sea turtles foraged by excavating

nutrient-rich rhizomes of seagrasses. Under high predation risks, they changed their foraging tactics, which stimulated slow-growing pioneer species and enhanced carbon stocks.

Aquatic herbivores can also enhance methane emission through the damage of emergent plant stems (greylag geese (*Anser anser*) (Dingemans et al., 2011); grasshoppers (Petruzzella et al., 2015)). The stems of emergent macrophytes have well-developed lacunar systems for gas transport; hence, broken stems may act like "chimneys", providing an open connection between the sediment and the atmosphere that bypasses the water layer. On the other hand, herbivores can reduce methane emission through bioturbation and removal of submerged plant beds (Bodelier et al., 2006).

3.2.3 Coastal protection

Seagrasses, mangroves and saltmarshes offer important coastal protection and sediment stabilization services. For seagrasses this function is generally attributed to seagrass canopy properties (Hendriks et al., 2010) and could be altered by herbivory. Although intensively grazed seagrass meadows have been shown to maintain their capacity for effective sediment stabilization, this function degrades when herbivores switch to belowground grazing , which causes decreased bed elevation, erosion and reduced coastal protection (Christianen et al., 2013). Similarly, livestock grazing can lower saltmarshes' accretion rates (Nolte et al., 2015), weakening the resilience and coastal protection function of these systems.

3.2.4 Habitat for other organisms

Macrophytes play an important role in structuring aquatic communities because they provide physical structure, increase habitat complexity and heterogeneity, affect oxygen and nutrient concentrations and provide refuge from predation (Carpenter and Lodge, 1986; Jeppesen et al.,

1998). Macrophytes also release dissolved organic carbon (DOC) which can be used by microbes in the periphyton or plankton (Findlay et al., 1986). Therefore, by consuming macrophytes, herbivores may deteriorate the habitat for other organisms. Fish productivity was found to be lower in seagrass meadows grazed by green turtles (Arthur et al., 2013) and after meadow collapse caused by overgrazing (reported for turtles in (Christianen et al., 2013). Similarly, herbivorous fishes, dugongs, geese and other waterbirds have been found to drastically reduce invertebrate biomass in seagrass meadows and salt marshes (Marklund et al., 2002; Sherfy and Kirkpatrick, 2003; Skilleter et al., 2007; Pages et al., 2012) . Impacts on invertebrates may occur even where the proportional reduction of vegetation is low (Bortolus et al., 1998).

3.2.5. *Primary production*

Submerged and emergent macrophytes can significantly contribute to the primary production of aquatic ecosystems (Blindow et al., 2006; Brothers et al., 2013). This holds especially for small lakes which represent approximately 99% of all lakes (Downing et al., 2006; Verpoorter et al., 2014). Direct studies on the effect of herbivory on aquatic plant growth and production are scarce because quantification of the impact of grazing rates on plant production requires coupled measurements of age-dependent grazing loss and turnover rate of plant tissue (Sand-Jensen et al., 1994). In general, fast turnover of the plant tissue (i.e. high specific growth rate) can compensate for intense herbivory under non-limiting resource conditions (Sand-Jensen and Jacobsen, 2002). Cherry & Gough (2009) found that *Nymphaea odorata* may tolerate moderate levels of herbivory by reallocating biomass and resources aboveground. On the contrary, stands of *Myriophyllum spicatum* retract their resources to belowground parts after defoliation by aquatic caterpillars (Miler and Straile, 2010). Water hyacinths (*Eichhornia crassipes*) were also found to fully compensate for low levels of continuous defoliation, regardless of nutrient availability (Soti and Volin, 2010). In seagrass ecosystems, reported effects of large herbivores were positive for intermediate densities of green

turtles (e.g. an increased tolerance to eutrophication), and negative for high densities of green turtles (e.g. switch to belowground grazing causing meadow collapse) (Christianen et al., 2012; Christianen et al., 2013). Similarly, moderate levels of simulated fish herbivory stimulated seagrass in primary production (i.e. compensatory growth), while very high levels of herbivory decreased it (Verges et al., 2008).

At whole-ecosystem level, herbivory on submerged macrophytes may have different effects on gross primary production (GPP). If herbivory results in a shift from clear-water to turbid conditions (see below), GPP can be expected to decline, at least under intermediate concentrations of total phosphorus (Brothers et al., 2013). On the other hand, large grazers that remove old seagrass leaves covered in ephiphytes and have been reported to increase primary production (Valentine et al., 1997; Moran and Bjorndal, 2005; Christianen et al., 2012).

3.2.6. *Regime shifts*

Shallow eutrophic lakes and lowland rivers may exist in two alternative stable steady states, a clear-water state dominated by submerged macrophytes and a turbid, phytoplankton-dominated state (Scheffer et al., 1993; Hilt et al., 2011; Hilt, 2015). In deeper lakes, submerged macrophytes may also contribute to the stabilisation of clear-water conditions (Hilt et al., 2010; Sachse et al., 2014). Shifts between clear-water and turbid states have been attributed to changes in nutrient loading, in the abundance of zooplanktivorous fish (e.g. by biomanipulation) and/or in macrophyte cover (Scheffer et al., 1993; Sondergaard et al., 2007; Bakker et al., 2010). Herbivory on macrophytes may also play a significant role for shifting macrophyte-dominated systems into the turbid state, or preventing the shift from turbid- into clear-water conditions. Mitchell & Wass (1996a) concluded that the cumulative effect of waterfowl grazing consumption was small but might become critical when other conditions for macrophyte growth become limiting (due e.g. to light limitation caused by high water turbidity). A recent modeling study indeed showed that herbivory on macrophytes often becomes

important in combination with additional stress by periphyton shading (Hidding et al., 2016). Herbivory by birds and fish may thus trigger the loss of submerged vegetation under high nutrient loading (Van Donk and Otte, 1996; Paice et al., in press), possibly in combination with other stress factors. Similarly, after reductions in nutrient loading, herbivorous birds may inhibit the expected recovery of macrophytes (Lauridsen et al., 1993; Søndergaard et al., 1996; Hilt, 2006).

4. Perspectives: historical and future changes in herbivore grazing pressure

Herbivore management and global environmental change, including water level fluctuations, eutrophication, temperature rise and invasive species, feedback on herbivore numbers, herbivore distribution and grazing pressure.

4.1 Changes in herbivore assemblages over time

There is a growing body of evidence that herbivore assemblages have varied over time considerably in their diversity and abundance, and are likely to continue to vary in the future. Throughout human history, people have exploited many aquatic herbivore species, including waterfowl, Sirenians, beavers, and muskrats, for food, recreation, and animal products such as skins, furs, feathers, and oils (Domning, 1982; Kitchener and Conroy, 1997). Human overexploitation has had catastrophic effects on many herbivore populations, with a wide range of species experiencing reduced population sizes and geographic ranges, and even extinction (Jessen, 1970; Turvey and Risley, 2006). Profound historical changes in herbivore assemblages were particularly evident in shallow seas and coastal habitats, where the diversity and distributions of mammalian mega-herbivores (Sirenians such as manatees and dugongs) were reduced heavily due to hunting by humans (Whitehead, 1978; Jackson, 1997; Turvey and Risley, 2006; McCauley et al., 2015). Freshwater systems have also seen

531 the loss of many large-bodied herbivore species, in particular mammals (Moss, 2015; Bakker et al.,
532 2016b). Additionally, during the twentieth century a range of semi-aquatic herbivore species
533 switched from aquatic to terrestrial feeding, particularly during winter (Laubek, 1995), further
534 reducing herbivore abundance and diversity within aquatic systems. Such habitat shifts have been
535 most widely documented for avian herbivores such as species of swans, geese, ducks and rails
536 (Jefferies et al., 2003; Van Eerden et al., 2005). The substantial effects of humans on aquatic
537 herbivores meant that the twentieth century represented a low point for herbivore abundance and
538 diversity across aquatic systems. Indeed, we find it interesting to note that earlier authors drew their
539 conclusions on the apparent unimportance of plant-herbivore interactions in aquatic ecosystems
540 based on research conducted during a period in which aquatic herbivores were relatively scarce. For
541 Carribean coastal ecosystems it has even been documented that these were severely degraded long
542 before ecologists began to study them, through the decimation of large vertebrates including green
543 turtles and manatees by about the year 1800 (Jackson 1997).

544 Stricter hunting regulations and conservation efforts in the second half of the twentieth century have
545 facilitated recoveries in the range and population sizes of many key aquatic herbivore species (Nolet
546 and Rosell, 1998). An example is the Eurasian beaver (*Castor fiber*), reduced by overhunting at the
547 beginning of the twentieth century to c.1200 individuals in eight isolated populations across Europe
548 (Nolet and Rosell, 1998; Halley and Rosell, 2002). Following greater legal protections from hunting,
549 the Eurasian beaver underwent sustained population recovery and has re-established populations in
550 all areas within its former natural range (with the exception of Portugal, Italy, and the southern
551 Balkans), with a total population of at least 1.04 million individuals (Halley et al., 2012). Many species
552 of herbivorous waterfowl in temperate regions have made similar recoveries (Bellrose, 1976; Ankney,
553 1996). Of the 21 goose species (*Anser* spp. and *Branta* spp.) for whose long-term population trends in
554 Europe are known, 16 species are currently increasing (Fox et al., 2010). Recent changes in
555 agricultural practices have resulted in greater terrestrial food availability for overwintering
556 waterfowl, with larger species benefiting more in terms of population growth (Jefferies et al., 2003;

557 Van Eerden et al., 2005). Although many reptilian herbivores remain endangered, certain species
558 such as the green turtle (*Chelonia mydas*) have recently shown signs of population recovery in
559 response to three decades of conservation efforts (Chaloupka et al., 2008).

560 The recovery of species of aquatic herbivores has been aided by the recent interest in rewilding
561 ecosystems (Donlan et al., 2006). The key roles that extinct or extirpated large herbivores played in
562 the structure and functioning of terrestrial ecosystems has received growing recognition from
563 researchers (Donlan et al., 2006; Sandom et al., 2014; Bakker et al., 2016a; Doughty et al., 2016).
564 Recently, it has been proposed that large herbivores may have played equally-important roles in
565 regulating the structure and functioning of aquatic ecosystems (Moss, 2015; Bakker et al., 2016b).
566 Species of aquatic herbivore which can act as ecosystem engineers, such as the beaver, are typically
567 prime candidates for rewilding projects due to the wider ecosystem benefits that result from such
568 engineering (Collen and Gibson, 2001). The recent finding that beaver's creation of ponds increased
569 the diversity of herbivorous waterfowl within the landscape indicates that natural recolonization and
570 rewilding may result in wider changes to herbivore assemblages than the target species alone,
571 through the facilitation of different herbivore taxa (Nummi and Holopainen, 2014).

572 The recovery of predator populations, via natural recovery and conservation efforts, can also affect
573 plant-herbivore interactions (Estes et al., 2011). Evidence from terrestrial and marine systems shows
574 that herbivore impacts on plants can be reduced as predator numbers recover, because predators
575 not only lower herbivore abundance through direct consumption, but also alter herbivore
576 distributions and reduce grazing intensity through indirect effects of predator avoidance behavior
577 ('landscape of fear' *sensu* (Madin et al., 2011; Kuijper et al., 2013). Similar results could be found for
578 interactions between predators, herbivores, and macrophytes in aquatic systems, but little research
579 has been carried out to date. For example, a recent study found that green turtle (*Chelonia mydas*)
580 habitat use reflected trade-offs between food resources, body condition, and risk of predation by
581 tiger sharks (*Galeocerdo cuvier*) in seagrass beds (Heithaus et al., 2007). A decline in tiger shark

582 numbers may thus result in a strong increase of green turtle grazing on seagrass beds, potentially
583 resulting in a seagrass bed collapse (Heithaus et al., 2014).

584

585 *4.2 Exotic herbivore species*

586 The spread of non-native species has been a key driver of temporal changes in aquatic herbivore
587 assemblages in recent decades. A wide range of herbivore taxa have established invasive populations
588 known to impact on native macrophytes. Well-documented examples include birds such as the mute
589 swan in North America (Tatu et al., 2007), mammals such as the muskrat in Europe (Danell, 1979;
590 Sarneel et al., 2014), fishes such as the lessepsian rabbitfishes in the Mediterranean (Verges et al.,
591 2014a), molluscs such as the golden apple snail in Asia (Carlsson et al., 2004), and crustaceans such
592 as red swamp crayfish in Europe (Gherardi and Acquistapace, 2007; Van der Wal et al., 2013). Despite
593 attempts to prevent species transfer and establishment through improved biosecurity, rates of
594 invasion remain at a historic high (Cohen and Carlton, 1998; Jackson and Grey, 2013).

595

596 *4.3 Climate change and temperature rise*

597 Future environmental change is also predicted to alter herbivore assemblages. In particular, climate-
598 driven factors such as sea-level rise and changes in vegetation phenology and abundance have the
599 potential to alter where, when and how much herbivores feed, and thus have the potential to alter
600 plant-herbivore interactions across aquatic systems (Stillman et al., 2015). For example, northward
601 shifts in wintering range in response to warming have been recorded for several waterfowl species,
602 including semi-aquatic herbivores like greylag geese (Ramo et al., 2015). Furthermore, food
603 requirements change with temperature. With increasing temperatures, the energy requirements of
604 temperate ectotherm animals increase and they consume more food. Furthermore, they may change
605 their diet in response to temperature, which has consequences for the degree of plant consumption.

606 Omnivorous fish increase their relative consumption of plant material with increasing temperatures
607 (Prejs, 1984; Behrens and Lafferty, 2007, 2012), a pattern that is recently also found in copepods
608 feeding on seston (Boersma et al., 2016). For endotherms this pattern may be the opposite, as their
609 energy requirements decrease with increasing temperatures, but this hypothesis awaits empirical
610 testing. Warmer temperatures may also induce higher periphyton shading of macrophytes (Mahdy et
611 al., 2015), making them more prone to herbivory (Hidding et al., 2016).

612

613 *4.4 Herbivore impacts under human control*

614 Where herbivore impacts on macrophytes affect human activities, such as conservation, recreation,
615 and aquaculture, they may be viewed as undesirable. In most cases it should be noted that problems
616 caused by herbivores are often the direct or indirect consequence of earlier human actions. For
617 instance, ongoing eutrophication of lakes reduces the resilience of submerged plant beds to grazing
618 due to increased shading by periphyton which profits from the nutrient loading (Hidding et al., 2016),
619 and re-establishment of submerged vegetation can be inhibited by grazers as well (Hauxwell et al.,
620 2004). The combined hunting of large predators and the creation of marine protected reserves, as
621 the place where large herbivores are safe, has locally resulted in very strong grazing pressure on
622 seagrass beds by green sea turtles (Christianen et al. 2014).

623 Such herbivore impacts can lead to conflicts between people interested in herbivore welfare and
624 conservation, and those interested in the activity being affected by the herbivore (Redpath et al.,
625 2015). To date, conflicts have arisen due to overgrazing by reptilian, mammalian, and avian
626 herbivores (Table 2). In contrast, we could find no evidence of conflicts associated with invertebrate
627 herbivory, which may reflect differences in human values rather than ecological impact. Indeed,
628 evidence from a recent meta-analysis showed that vertebrate herbivores do not have consistently
629 greater impacts on macrophytes than invertebrate herbivores (Wood et al., 2016). Vertebrate
630 herbivores such as waterfowl, turtles, and Sirenians are often considered charismatic, and attempts

631 to manage their numbers, behaviour or distributions are likely to attract more opposition from
632 conservation and welfare groups than the management of invertebrate herbivores (Bremner and
633 Park, 2007; Small, 2012). Consequently, it can be difficult to implement management to alleviate the
634 effects of overgrazing (Coluccy et al., 2001).

635 Despite these conflicts, not all herbivore impacts on macrophytes are viewed as negative by people.
636 Herbivores have proven to be effective biocontrol agents to help reduce and eradicate undesirable
637 macrophytes, such as overabundant or invasive species (Newman, 2004; Cuda et al., 2008). A wide
638 range of herbivore biocontrol agents have been used globally (Table 3). Biocontrol of macrophytes
639 through herbivory has received growing interest from researchers and managers, particularly as
640 some biotypes of invasive macrophytes (e.g. *Hydrilla verticillata*) have developed resistance to
641 commonly-used herbicides (Cuda et al., 2008). More targeted biocontrol can be achieved by
642 invertebrate herbivores, which typically show greater specificity for macrophyte species relative to
643 vertebrate herbivores (Lodge, 1991; Newman, 1991). Since Wilson (1964) argued that "no insects
644 have yet been used for the biological control of aquatic weeds", a wide range of species of
645 coleopteran, lepidopteran, and dipteran biocontrol agents have been used successfully (Newman,
646 2004; Cuda et al., 2008). Both the conflicts related to overgrazing, and the use of herbivores as
647 biocontrol agents, show the importance of improving our understanding plant-herbivore
648 interactions. For example, understanding the density-dependence of herbivore impacts on
649 macrophyte abundance can inform the densities of biocontrol agents required to reduce
650 overabundant macrophytes (Cuda et al., 2008), or allow lake managers to predict the response of
651 macrophytes to changes in wild herbivore density (Wood et al., 2012a).

652

653 ## 5. How to improve understanding of herbivore impacts

654 *5.1 Bottom-up versus top-down control across environmental gradients*

Lodge (1991) ended his review with the conclusion that "To understand the influence of herbivory (relative to other biotic and abiotic factors) on macrophyte populations and assemblages, extensive comparisons of grazing damage across environmental gradients and across macrophyte and grazer species must be made." Whereas meta-analyses have provided valuable insight in the impact of different herbivores both on Angiosperms and macro-algae (Poore et al., 2012; Wood et al., 2016), and the relationship between macrophyte palatability and herbivore impact received increasing attention during the last decade, the variation in the intensity and impacts of herbivory along environmental gradients has been scantly explored. Bakker and Nolet (2014) suggested that herbivore impact may increase at nutrient-rich conditions, due to a combination of higher plant palatability and lower tolerance to grazing damage caused by additional stress factors (such as reduced light availability due to periphyton shading (Hidding et al., 2016). In an experimental pond system, herbivory by mallards proved to have stronger impact on submerged macrophytes under eutrophic than under oligotrophic conditions. We are not aware, however, of any field tests for this theory. Alternatively, herbivores may facilitate submerged macrophytes with increasing eutrophication, for example when moderate densities of small grazers such as freshwater snails clean submerged plants from epiphytes, which becomes more important under eutrophic conditions (Bakker et al., 2013). Also, when intense grazing stimulates the formation of new shoots, which are not yet colonized by epiphytes, large grazers such as green sea turtles, can compensate the negative effect of eutrophication for seagrass growth to a certain extent (Christianen et al., 2012).

5.2 Integrating marine and freshwater studies

Traditionally, freshwater macrophytes and seagrasses have largely been studied separately. To date, the literature on freshwater and marine herbivore impacts have not been integrated, and have largely developed separately despite the obvious areas of overlap. If cross-system comparisons were being made, these were often marine-terrestrial or freshwater-terrestrial comparisons and can

include both vascular plants and algae (Hay, 1991; Elser et al., 2000; Burkepile, 2013). This is unfortunate because, leaving a few obvious differences apart (such as the higher salinity and connectivity of marine systems), the ecology of marine and inland-water vascular macrophytes shows very few differences. Yet, integrative work on freshwater and marine vascular macrophytes still awaits its moment.

5.2 Herbivore assemblages: towards functional groups

For a better understanding of herbivore impact, researchers should consider the whole community of herbivores, which compete and facilitate each other. This has already been done for terrestrial systems long ago (McNaughton, 1985), but examples for aquatic systems are rare. One such example is the herbivore community in a shallow freshwater lake that forages on pondweed beds, consisting mainly of *Potamogeton pectinatus*. The sprouting plants are being grazed by resident waterfowl species like mute swans (*Cygnus olor*), mallards (*Anas platyrhynchos*), gadwall (*Anas strepera*) and coots (*Fulica atra*). The intensity and timing of grazing determine how much above-ground plant material is remaining and growing (Hootsmans, 1999). At the end of the summer, below-ground tubers are being formed depending on the amount of above-ground plant material (Van Wijk, 1988). Thus, more and, notably, earlier waterfowl grazing in summer results in less tuber biomass in autumn (Klaassen et al., 2006; Gyimesi et al., 2011). In autumn, tubers are being depleted by migratory swans (Bewick's swans *Cygnus columbianus*) and diving ducks (mainly tufted ducks *Aythya fuligula* and pochards *Aythya ferina*) until a grazing threshold (Nolet et al., 2001). The diving ducks benefit from the trampling activity of the swans, without negatively affecting the swans' intake rate; this therefore classifies as commensalism (Gyimesi et al., 2012). In accordance with a sequential population model (Jonzén et al., 2002), highest tuber biomass and in particular tuber production was generally found at sites foraged down to intermediate thresholds in the previous autumn. In this system a positive

705 feedback between tuber grazing and tuber production resulted from a reduction in self-shading or a
706 decrease in neighbour competition (Nolet, 2004).
707
708 Together, the interactions within herbivore communities will determine the effect of herbivore
709 diversity, a topic rarely touched upon in aquatic vascular plant beds (but see marine macro-algae and
710 seagrass systems, e.g (Duffy et al., 2003; Burkepile, 2013). Whereas all interactions at the species
711 level are interesting, a way forward can be to generalize beyond species by grouping herbivores in
712 guilds or functional groups and working out which traits best explain their relative effects. Such traits
713 could include body size, diet (herbivory-omnivory), habitat (terrestrial-aquatic linkages), migratory
714 strategy (sedentary versus migratory) and movement ecology (foraging ranges). Recently, grouping
715 of large savanna herbivores proved to be useful to understand their ecosystem impacts (Hempson et
716 al., 2015). Similarly, the ecosystem functions of aquatic large herbivores may be understood from
717 their habitat use, in particular how dependent on the aquatic systems they are in combination with
718 their movement ecology (Bakker et al., 2016b).
719

720 5.3 *Tools to study herbivore impacts*

721 Practically, the high variance in estimates of macrophyte abundance, even within a single study
722 system, can make herbivore effects difficult to detect in aquatic systems without large sample sizes
723 (Wood et al., 2012b). However, numerous methods have been developed and employed to detect
724 and/or quantify herbivory on macrophytes and seagrasses (Table 4). The most direct approach for
725 detection and quantification of effects is a technique known as tethering (Kirsch et al., 2002; Tomas
726 et al., 2005; Prado et al., 2007; Pages et al., 2014). With this technique it is possible to estimate the
727 biomass (or cm of leaf) eaten daily, i.e. direct herbivory rates (see Table 4). Another direct approach
728 to detect and quantify herbivore effects are in situ exclosure cages with subsequent biomass
729 measurements in- and outside.

730 Other less direct herbivory detection and quantification methods focusing on macrophytes include
731 visual estimations of leaf damage and measurements of macrophyte performance across naturally-
732 occuring spatial or temporal gradients in herbivore assemblage properties (e.g. density) (Table 4).
733 Aerial photographs taken from drones (Brandt et al., 2015), echo-sounding (Jäger et al., 2004) and
734 remote sensing (Silva et al., 2008) may increasingly being used in the future for larger scale
735 quantifications of macrophyte consumption by herbivores. At the herbivore side, underwater videos,
736 aquarium feeding experiments, molecular markers, stable isotope signatures, gut and faeces
737 analyses, and whole-lake fish telemetry have been applied (Table 4).

738 Finally, mechanistic models allow assessments of herbivory over larger spatial and temporal scales
739 than field-based methods, e.g. long-term predictions of future herbivory. They initially need to be
740 tested against field data to demonstrate accuracy and have been developed for both, the herbivores
741 and the plants (Table 4). Recently, a plant growth models for a specific macrophyte species has been
742 used to detect a synergy between herbivory and shading by periphyton as additional stressor
743 (Hidding et al., 2016). Simulation models of herbivore foraging can be useful tools to predict foraging
744 impacts, and test strategies for grazing management (Wood et al., 2014a; Nolet et al., 2016).

745

746 **6. Conclusions**

747 Over the last 25 years, a substantial body of evidence has developed that shows that herbivory is an
748 important factor in the ecology of macrophytes across freshwater and marine habitats. Compiling the
749 most recent data, we conclude that herbivore impacts in freshwater and marine ecosystems are
750 typically 5-10 times greater than those reported for terrestrial ecosystems. This corresponds with
751 lower C:N stoichiometry of submerged aquatic plants. Furthermore, aquatic habitats are
752 characterized by large variation in grazing pressure. Considerable changes have occurred, and are
753 predicted to occur, in herbivore diversity and abundance, with wide implications for the composition
754 and dynamics of macrophyte communities, as well as for the structure and functioning of aquatic

ecosystems. There are pressing needs to improve our management of undesirable herbivore impacts on macrophytes (e.g. leading to an ecosystem collapse), and the conflicts between people associated with the impacts of charismatic mega-herbivores. While simultaneously, the long-term future of maintaining both viable herbivore populations and plant beds should be addressed, as both belong in complete ecosystems and have co-evolved in these long before the increasing influence of man.

Most research to date has focused on the short-term impacts of herbivores on macrophyte abundance and community composition. To understand the roles of herbivores more fully we need to consider their longer-term impacts and the role of herbivory in the (co-)evolution of both macrophyte and herbivore species. Furthermore, a better integration of the freshwater, marine, and terrestrial herbivory literatures would greatly benefit future research efforts.

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Captions to figures

Figure 1. Frequency diagram of percentage of herbivory (% herbivory) on vascular plants (a: mean percent damage; b, c: net primary production removal) and biomass C:N ratio (g/g) across (a,d) terrestrial, (b,e) freshwater and (c,f) marine ecosystems. Freshwater and marine data include both submerged and emergent plants. The median values in each panel are indicated with an arrow accompanied by "M".

Data sources: terrestrial (a) herbivory: percentage of leaf area damaged (Turcotte et al. 2014), (d) biomass C:N ratio: in foliage (Elser et al. 2000); freshwater (b) herbivory: percentage of emergent and submerged vascular plant biomass removed by herbivores in herbivore exclosure/enclosure or addition/removal experiments (Wood et al. 2016), (e) biomass C:N ratio: in submerged and emergent vascular plants (Cloern et al. 2002; Bakker unpublished data); marine, (c) herbivory: percentage of emergent and submerged vascular plant biomass removed by herbivores in herbivore exclosure/enclosure or addition/removal experiments (Wood et al. 2016), percentage of leaf area damaged in seagrasses (Cebrian and Duarte 1998) (f) biomass C:N ratio: in seagrass leaves (Atkinson & Smith 1983, Duarte 1990, Fourqurean et al. 1993, Cebrian and Duarte 1998, Fourqurean et al. 2010, Olsen en Valiela 2010), in salt marsh plants (Cloern et al. 2002). The duration of the herbivroy studies varied from instantaneous measurements of percentage leaf damage in terrestrial plants and seagrasses to exclosures studies in freshwater and marine ecosystems ranging from about a week to multiple study years (study durations reported in Wood et al. 2016 who found no effect of study duration on percentage herbivore plant biomass removal).

Figure 2. Frequency diagram of net primary production removal (% herbivory) and biomass C:N (g/g) for vascular freshwater and marine macrophytes of different growth forms (emergent and

1484 submerged). Emergent plants include floating plants and wetland or salt marsh plants. The median
1485 values in each panel are indicated with an arrow accompanied by “M”. Data sources as in Fig. 1.

1486

1487 Figure 3. Synthesizing scheme indicating the effects of herbivores on macrophyte beds and the
1488 functioning of shallow freshwater (a) and marine (b) aquatic ecosystems. Herbivores affect plant
1489 abundance and species composition by grazing and bioturbation. Their presence alters
1490 biogeochemical cycling and primary production, they transport nutrients and propagules across
1491 ecosystem boundaries, modify habitat for other organisms and affect the level of shoreline
1492 protection by macrophyte beds. Symbols in the figure are courtesy of the Integration and Application
1493 Network, Univ. of Maryland Center for Environmental Science (ian.umces.edu/symbols/).

1494 Table 1. Plant and herbivore traits promoting propagule dispersal by aquatic herbivores.

1495

Trait	Effect	References
Herbivores		
Ability to chew or grind food	The presence of a gizzard or grinding teeth reduces propagule survival. Among waterfowl, heavier gizzards reduce seed survival but higher grit content may enhance germination of undigested seeds.	Figuerola et al. (2002)
Furry or sticky appearance of animal body	Animals with a surface on which propagules can attach disperse more propagules	
Diet selection	Targeted feeding on seeds may result in more transport, but also in more seed predation – thus reducing the transport through untargeted feeding which, particularly when mixed with large bulks of food (plant parts, animal food, debris), may result in high propagule survival.	Figuerola et al. (2003)
Travelling distance	Larger travelling distances results in further potential dispersal, particularly for migratory species that cover long distances in single leaps	Viana et al. (2013b)
Habitat use	Animals with specialized use of aquatic habitats are more likely to deposit the propagules in suitable habitat. In particular, targeted arrival to aquatic habitats at stopovers may increased the deposition of	Figuerola and Green (2005)

	propagules ingested at departure sites, especially after the first drinking and feeding bout.	
Plants		
Propagule dimensions	Small, round seeds survive digestive tract better than large, elongated seeds. Small size, in particular, may enhance ingestion mixed with vegetative plant material, increasing propagule ingestion ("foliage is the fruit", sensu Janzen (1984)) and survival to gut passage.	Mueller and van der Valk (2002); Soons et al. (2008); Figuerola et al. (2010)
Hardness and permeability of seed coat	Thicker, harder and less permeable seed coats increase survival to disperser's gut passage, but may reduce germination in the absence of uningested seeds.	Mueller and van der Valk (2002); Santamaria et al. (2002); Figuerola et al. (2010)
Adaptations for epizoochorous dispersal	Hooks, rough or sticky surface have been proposed to enhance dispersal potential	Van der Pijl (1982)
Resistance to dessication	Organism's and/or propagule's resistance to dessication may enhance epizoochorous dispersal of aquatic organisms	Panov and Caceres (2007); Havel et al. (2014)

1499 Table 2. An overview of reported conservation conflicts that have arisen from the impacts of overgrazing by herbivores on macrophytes.

1500

Herbivore	Issue	Parties in conflict	Location(s)	Duration	Current status	References
Green turtle (*Chelonia mydas*)	Overgrazing of seagrasses can undermine conservation efforts in protected areas and reduce fish catches for local people	Turtle and seagrass conservationists, fishermen	Indo-Pacific oceans	1980s - present	Ongoing	Arthur et al. (2013); Christianen et al. (2014)
West Indian manatee (*Trichechus manatus*)	Overgrazing has hindered efforts to restore submerged macrophyte beds	Manatee and macrophyte conservationists	Freshwater and brackish ecosystems in south-east USA	1990s - present	Ongoing	Hauxwell et al. (2004)
Beaver (*Castor spp*.)	Impacts on aquatic habitats, via effects on vegetation and wider ecosystem (e.g. fish)	Conservationists, animal welfare groups, fishermen, and statutory wildlife management	Freshwater habitats across North America, Russia	Unknown - present	Ongoing	Nolet and Rosell (1998); Collen and Gibson (2001); Halley and Rosell (2002)

		agencies				
Coypu (*Myocastor coypus*) and muskrat (*Ondatra zibethicus*)	Overgrazing on emergent macrophytes degrades aquatic habitats	Conservationists, animal welfare groups, and statutory wildlife management agencies	Freshwater lakes and wetlands in Europe	1930s – present	Resolved by 1970s via extirpation of coypu in Britain; ongoing elsewhere in Europe	Gosling and Baker (1989); Barends (2002)
Mute swan (*Cygnus olor*)	Overgrazing of macrophytes degrades aquatic habitats	Conservationists, animal welfare groups, and statutory wildlife management agencies	Freshwater habitats in Europe and USA	1950s - present	Ongoing	Perry and Perry (2008); Wood et al. (2014b, 2015)
Geese (*Anser* spp., *Branta* spp., and *Chen* spp.)	Overgrazing of emergent macrophytes degrades wetland habitats	Conservationists, animal welfare groups, and statutory wildlife management	Canadian Arctic and sub-Arctic wetlands, freshwater lakes	1970s - present	Ongoing	Kerbes et al. (1990); Nichols (2014)

		agencies	and wetlands in Europe and North America

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1504 Table 3. A summary of key herbivore taxa used as biocontrol agents in the management of macrophytes.

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Herbivore biocontrol agent	Target macrophyte(s)	Herbivore generalist or specific?	References
West Indian manatee (*Trichechus manatus*)	Wide range of macrophyte species, including *Cabomba aquatica*, *Anacharis* spp., *Leersia* spp., *Utricularia* spp.	Generalist	Allsopp (1960)
Geese (*Anser spp*)	Wide range of macrophyte species	Generalist	Ross (1971); Wilson et al. (1977)
Grass carp (*Ctenopharyngodon idella*)	Wide range of macrophyte species, including invasive species such as *Hydrilla verticillata*	Generalist	Clayton (1996); Hanlon et al. (2000)
Cichlid fishes, e.g. blue tilapia (*Oreochromis aureus*)	Wide range of macrophyte species	Generalist	Schwartz et al. (1986)
Crayfish, e.g. papershell crayfish (*Orconectes immunis*)	Wide range of submerged macrophyte species	Generalist	Letson and Makarewicz (1994)
Weevils, e.g. milfoil weevil	Species-specific biocontrol agents identified for many macrophyte	Specialist	Creed and Sheldon

(*Euhrychiopsis lecontei*), Hydrilla tuber weevil (*Bagous affinis*)	species, e.g. Hydrilla (*Hydrilla verticillata*), Eurasian water milfoil (*Myriophyllum spicatum*)		(1993); Newman (2004)
Apple snails (*Pomacea* spp.)	Wide range of macrophyte species	Generalist	Rushing (1973)
Dipteran larvae, e.g. Asian hydrilla leaf-mining fly (*Hydrellia pakistanae*)	Species-specific biocontrol agents identified for many macrophyte species, e.g. *Hydrilla verticillata*	Specialist	Wheeler and Center (2001); Bownes (2014)
Lepidopteran larvae, e.g. waterlettuce moth (*Spodoptera pectinicornis*)	Species-specific biocontrol agents identified for many macrophyte species	Both generalist and specialist species reported	Wheeler et al. (1998); Gross et al. (2001); Newman (2004)
Hemiptera, e.g. *Eccritotarsus catarinensis*	Species-specific biocontrol agents identified for many macrophyte species, e.g. Water hyacinth (*Eichhornia crassipes*)	Specialist	Coetzee et al. (2007); Hernandez et al. (2011)
Orthoptera, e.g. water hyacinth grasshopper (*Cornops aquaticum*)	Species-specific biocontrol agents identified for many macrophyte species, e.g. Water hyacinth (*Eichhornia crassipes*)	Specialist	Bownes et al. (2010)

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1508 Table 4. Different methodologies used to detect and quantify herbivory on macrophytes.

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Methodology	Explanation	References
Exclosures	Installation of cages (fully closed or open at the bottom) to protect macrophytes from different herbivores (fish, muskrats, waterfowl, crayfish, turtles)	Søndergaard et al. (1996); Körner et al. (2002); Hilt (2006); Christianen et al. (2012); Poore et al. (2012); Veen et al. (2013); Van der Wal et al. (2013); Sarneel et al. (2014)
Tethering	Shoot herbivory rates (cm shoot-1 day-1) are estimated for marked shoots by measuring leaf elongation over time.	Kirsch et al. (2002); Tomas et al. (2005); Prado et al. (2007); Pages et al. (2014)
Underwater videos	Video recording and quantification of fish activities including plucking of leaves	Körner & Dugdale (2003); Bennett & Bellwood (2011); Verges et al. (2014b)
Visual estimation of leaf damage		Francescini et al. (2010)

Natural gradients	Measure macrophyte performance (e.g. growth rate, biomass, etc) across naturally-occuring gradients in herbivore assemblage properties (e.g. density)	Wood et al. (2012b)
Drones	Identificaton of muskrat damage in constructed wetlands by digitizing low-altitude aerial photographs	Brandt et al. (2015)
Molecular markers	Assessments of genetic variation in plants across environmental or geographical (latitudinal) gradients using different molecular markers	Mader et al. (1998); Hangelbroek et al. (2002) ; King et al. (2002); Hidding et al. (2014)
Stable isotope analyses	Measurement of carbon, nitrogen and hydrogen stable isotopes in resources and consumers and application of mixing models	France et al. (1996); Solomon et al. (2011); Dorenbosch and Bakker (2012); Mendonca et al. (2013); Vander Zanden et al. (2013); Scharnweber et al. (2014); De Kluijver et al. (2015)
Gut analyses and stable isotope analyses	Gut analyses in fish combined with stable isotope analyses of basal food resources and fish	Mao et al. (2014)

Telemetry	Whole-lake fish telemetry	Hanson et al. (2007)
Bird counting and determination of lignin content in faeces		Dos Santos et al. (2012)
Laboratory feeding rate determination in fish	Determination of fish feeding rates in aquaria	Körner & Dugdale (2003)
Mechanistic models	Simulations of foraging herbivores or effects on plant growth can predict the location, timing, and magnitude of herbivore effects on macrophytes	Hootsmans (1999); Van Nes et al. (2003); Nolet et al. (2006); Wood et al. (2014a); Nolet et al. (2016); Hidding et al. (2016)

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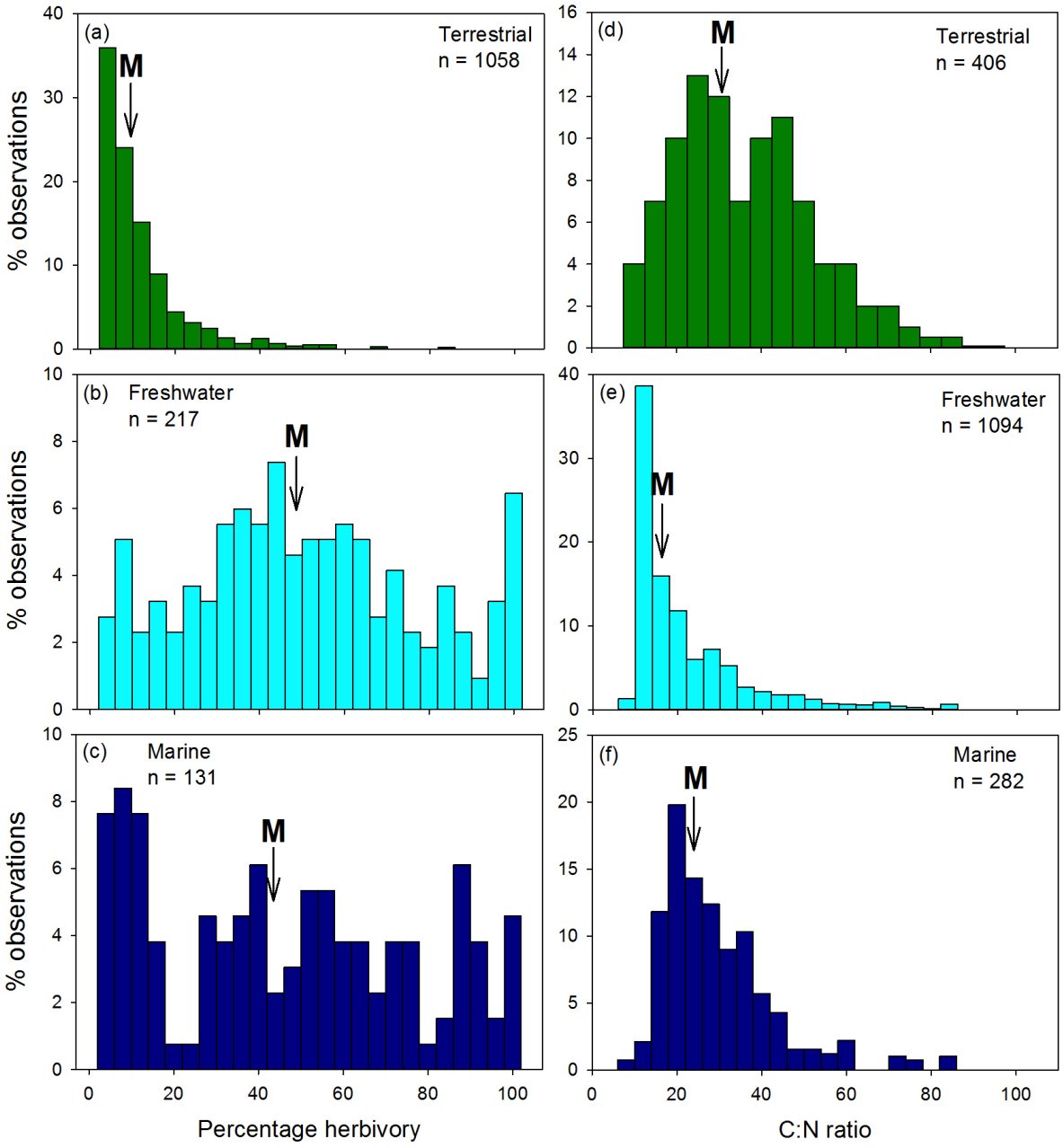
(a)
Terrestrial
n = 1058
M
(d)
Terrestrial
n = 406
M
(b)
Freshwater
n = 217
M
(e)
Freshwater
n = 1094
M
(c)
Marine
n = 131
M
(f)
Marine
n = 282
M
% observations
% observations
% observations
Percentage herbivory
C:N ratio

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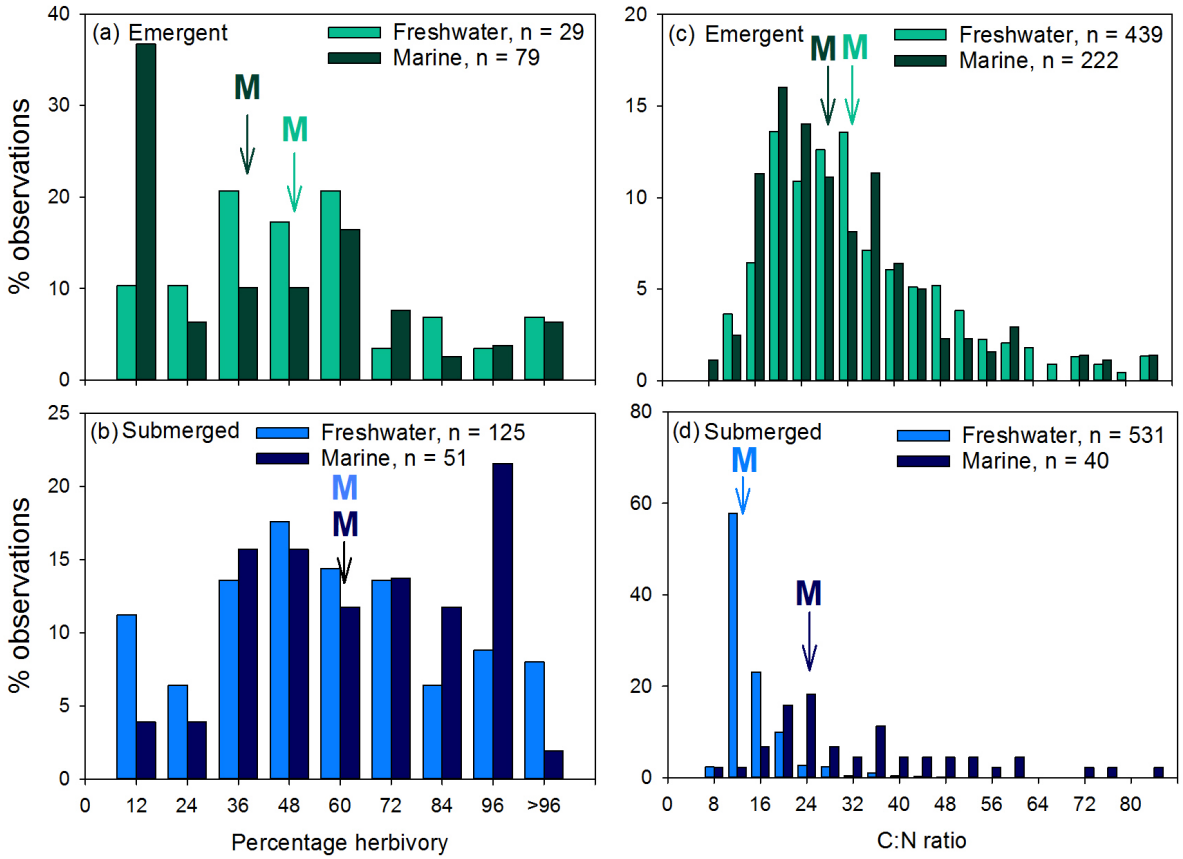
(a) Emergent
Freshwater, n = 29
Marine, n = 79
M
M
% observations
(c) Emergent
Freshwater, n = 439
Marine, n = 222
M
M
(b) Submerged
Freshwater, n = 125
Marine, n = 51
M
M
% observations
(d) Submerged
Freshwater, n = 531
Marine, n = 40
M
M
0 12 24 36 48 60 72 84 96 >96
Percentage herbivory
0 8 16 24 32 40 48 56 64 72 80
C:N ratio

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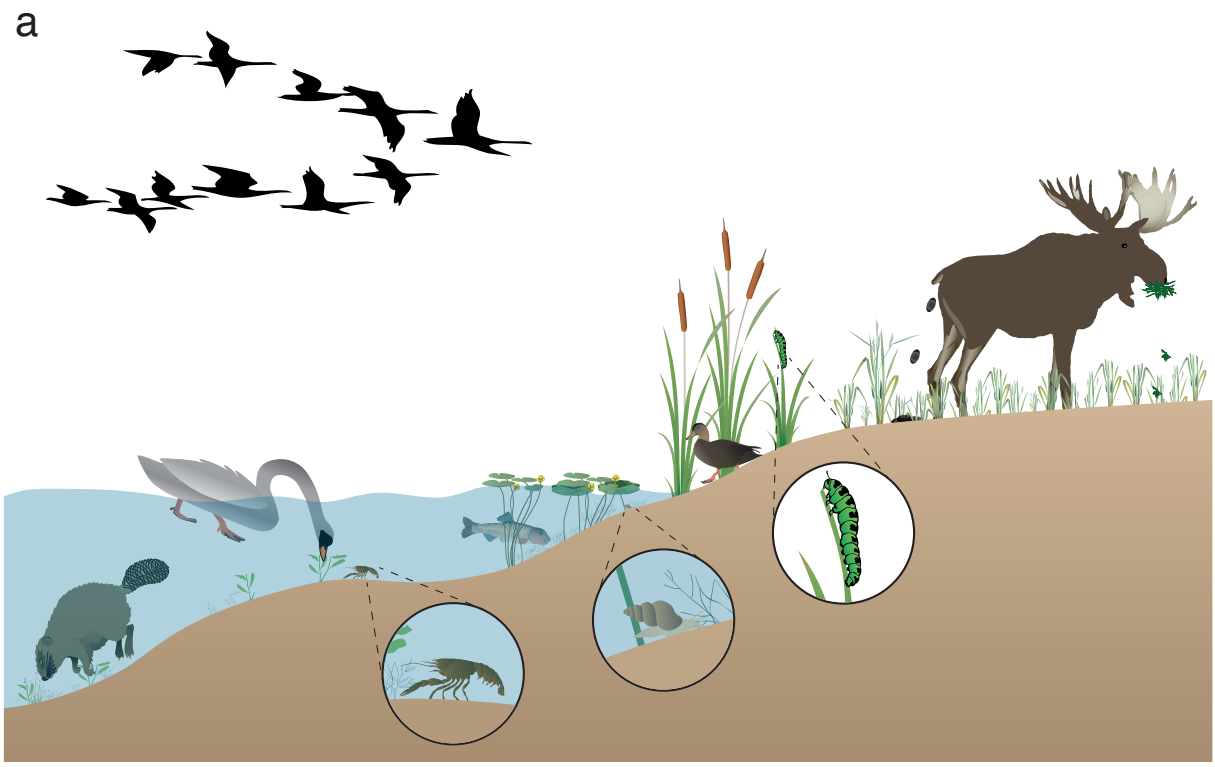

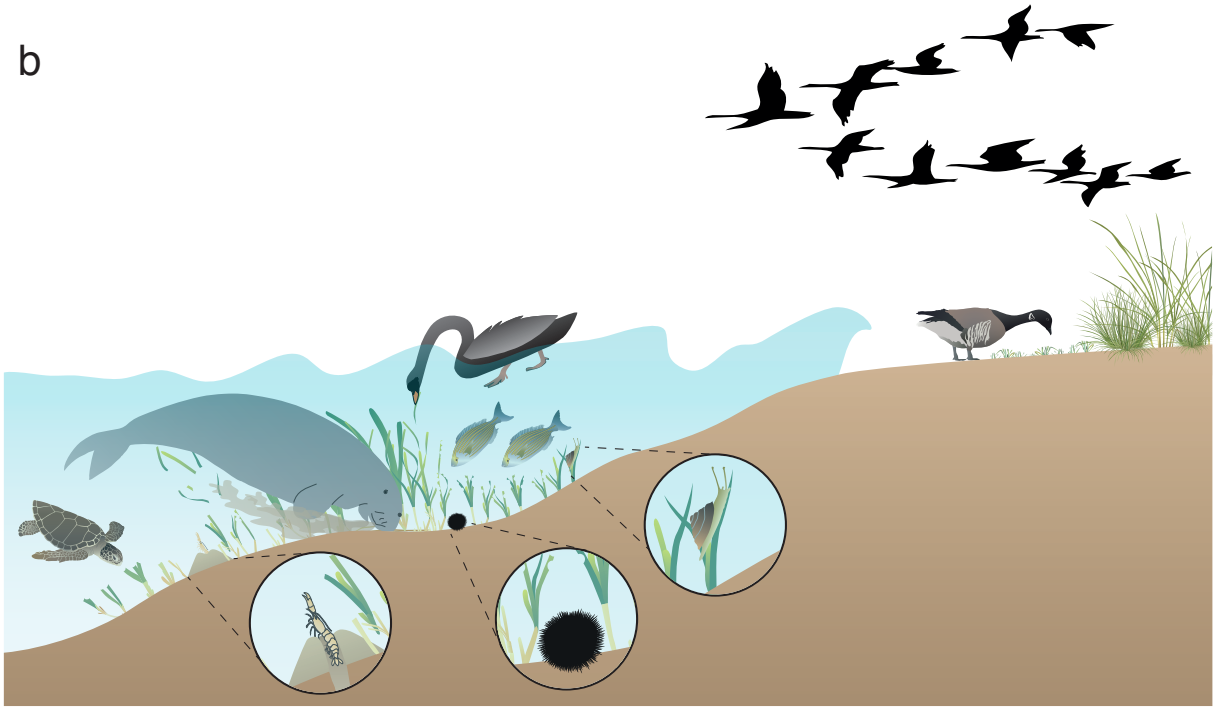

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